

6.

Some Variations in Grouping and Dominance Patterns Among
Birds and Mammals.

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(Text-figure 1).

The tendency to aggregate is of very general occurrence among animals. Aggressive behavior, in the sense of fighting or threatening and apart from predator-prey relations, is also of quite general occurrence, particularly among the more complex phyla of animals, and for the vertebrates there is sufficient evidence to indicate that aggressiveness is often regulated by means of dominance hierarchies or territorial relations (Collias, 1944; Allee, 1945). The nature of the relationship between the aggregation tendency and the various forms of aggressive behavior does not seem to have been sufficiently investigated and is of special interest since these two general phenomena are often opposed to each other. More information is needed on the relationship of aggressive-submissive dominance relations to grouping patterns.

Another problem concerns the generality and variations of intra- and interspecies dominance orders within given ecological habitats. Considerable data will be required before many generalizations on these topics can be considered secure, and one object of this report is to contribute and to cite additional data for birds and mammals.

These problems ideally should be worked out in the field under natural conditions; however, tentative solutions frequently can be obtained more rapidly from captive animals in large enclosures. Preliminary checking often reveals considerable similarity between the behavior of captive animals and of the same species in the wild. No doubt important differences exist, but at the least, studies on domestic and captive animals could serve as a basis for formulating working hypotheses for related studies in the field. Certainly the converse is also true.

More detailed comparison of the results of the present study with field studies will be made later in this article.

The New York Zoological Park maintains a great variety of birds and mammals in large enclosures, and these provided excellent material from which to choose suitable subjects for studies of grouping and dominance patterns.

For the first objective, the study of the relationship between dominance and grouping behavior, two groups of mammals and two of birds were chosen. A group of White-tailed Deer (*Odocoileus virginianus*) was studied as an example of a species which formed small, rather loose groups in which the individuals were often scattered widely over the enclosure. In nature these deer are said to form small groups which may break up at the end of winter; during the rut the buck is usually seen with one doe, occasionally with two or more (Seton, 1929, p. 278). In contrast, a group of Nyala antelopes (*Tragelaphus angasi*) was selected for study because these animals generally formed a compact herd unit. On the African veldt Nyalas live in small troops of one adult male and about half a dozen females. At certain times the females with their young and the immature males herd together, while the adult males wander off singly or in small groups (Fitzsimmons, 1920, p. 122). A small group of penguins gave an example of a species which breeds normally in large, gregarious and compact colonies in which small individual pair territories are marked. A flock of geese of several species gave an example of forms in which wider spacing of breeding pairs is the rule, and also provided opportunity to analyze the organization of a non-breeding and heterospecific flock.

For the second objective, which was to examine in some detail the generality of the dominance principle in a variety of animals from given ecological habitats, observations on the three groups selected were less detailed and systematic. The goose enclosure mentioned above provided an example of a pond habitat, and contained several species of geese, ducks and cranes. A large flying cage contained marsh birds such as herons, ibises and spoonbills as well as many other native and exotic species. A large and grassy

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enclosure, known as the "African Plains," contained birds and mammals from the African veldt.

GENERAL PROCEDURE.

Grouping relations between the individuals of each species were estimated on the basis of repeated observation. In general these grouping patterns were easily observed and appeared to be quite definite and consistent, and therefore little attempt was made to enumerate instances of contiguity between particular individuals. In a few instances, as in the case of the flock of geese, such impressions of grouping relations were checked by frequent mapping of the relative places occupied by the different individuals when the flock was resting or sleeping.

Dominance relations between individuals were ascertained by enumeration of observed instances of aggressive-submissive interactions, of each individual with all the others. Many but not all of these instances occurred during competition over bits of food provided by the observer or by the caretaker. One animal would attack or threaten another, driving it from the food, and the latter individual was thereupon adjudged subordinate in this particular encounter. In some instances, as in the case of the antelope, aggressive-submissive interactions were observed between males in the proximity of females quite independently of the food supply. In certain other instances of aggressive-submissive interactions, particularly involving penguins, the cause of the interaction was not very evident.

Since for any given pair of individuals in successive encounters the same animal with very few exceptions always dominated the other, it was not difficult to gather sufficient data to establish the great majority if not all of the dominance relations within the group. It was sometimes difficult to ascertain the dominance relations of animals at or near the bottom of the hierarchy since such individuals frequently avoided active competition with the others.

It was more or less obvious to repeated observation that many of the aggressive-submissive encounters of the penguins involved defense of a given area or territory by the owner, and the location of such encounters was added to the tabulation in an attempt to determine the center and limits of the territory. In practice, the territory was determined by noting the area most frequented by a given individual and the degree of its dominance over other individuals on this area. Exceptions to dominance on its usual territory by a given individual were rare, but not infrequently, the presence of other individuals on the more peripheral parts of the territory would be tolerated.

Each group of animals was observed at irregular hours and almost every day. Observation periods for the White-tailed Deer were 15 to 30 minutes long and totalled seven hours from August 4 to September 4.

The Nyalas were watched for some 13 hours from August 6 to September 2; as a rule observation periods were 30 minutes long for each day of observation. The penguins were observed for a total of 126 hours between June 21 and September 4. The usual length of the observation period was one hour, but this varied considerably; there was one full day period of observation. The geese were watched from June 23 to September 6, during 61 observation periods, for 38 hours, including one full day. The usual daily observation periods for the geese were either 15 or 30 minutes long. The wading birds in the large flying cage were generally watched for 30 minutes on any one day. Altogether there were 12 such observation periods, making a total of six hours from August 11 to September 3. The birds and mammals of the African Plains were watched simultaneously with the Nyalas whenever they happened to come to the vicinity of these antelopes. Otherwise they were observed more casually and at irregular times.

WHITE-TAILED DEER.

Description of the White-tailed Deer Group. This group consisted of two adult eight-point bucks, one spike buck and six adult females. Four fawns were dropped about a month before observations began.

Identification of individuals was relatively easy in the case of the three males because of the form of the antlers. They are here denominated Buck One (B_1), Buck Two (B_2) and Spike (Sp). In the case of the does, reliance for identification was placed chiefly upon minor differences in coloration or markings. One was named Scar (Sc), the others are denominated White Nose (Wn), Black Nose (Bn), Pale (gray) Nose (Pn), Dark (gray) Nose-Dark Chin (Dnd) and Dark Nose-Light Chin (Dnl).

The history of the group was known to some extent. All deer were removed from the paddock in the spring of 1943, leaving three hand-reared does which could not be caught. About this same time Buck One was received as a fawn and he and the original does are the parents of the other deer with the exception of one tame female given to the Zoo in 1946. This last female tended to keep somewhat apart from the others. Two does were born in the spring of 1945, as was Buck Two. Buck Two was a two-year-old and the spike buck was a little over one year of age when the study began. Unfortunately, in the case of the females, it was not possible to identify the age records for each individual.

The enclosure was roughly rectangular in shape, some 400 feet long by approximately 300 feet wide, giving the deer a range of about three acres. It contained many large deciduous trees but virtually no undergrowth or low ground cover except for a couple of large trees that had been felled near the center of the enclosure. The ground was somewhat rocky and quite uneven, almost

hilly in places. Along one side of the enclosure there flowed a small artificial stream. In addition to the White-tailed Deer, a bull Moose and two cow Moose occupied the enclosure.

Grouping Relations. As a rule the White-tailed Deer were scattered widely over the enclosure, either singly or in groups of twos or threes, occasionally of more individuals. There was no observable consistent association of any pairs during the summer. The deer were more likely to congregate somewhat while being fed or while resting, but even then some of the individuals were likely to be in other parts of the paddock.

Dominance Relations. Nothing like defense of local areas (territorialism) within the enclosure was seen, but the deer were observed to be ranked according to a definite dominance hierarchy (Table I). Morsels of bread or small pieces of carrot were thrown in among the deer and when they were hungry one would drive the others from the particular bit of food. A doe would abruptly raise one foreleg, bending it at the knee and kicking it forward at a subordinate; if the latter proved recalcitrant, as was occasionally the case, she might then rear up on her hind legs and strike out with both forefeet. However, no fights were seen. The bucks occasionally used the same method but usually they threatened subordinates by dropping the head and lunging at them with the antlers. Rarely a doe was heard to make a low harsh noise or bleat while threatening a subordinate. When threatened, subordinates would retreat and either return, keeping at a safe distance, or else apparently lose interest in the food and move to some other part of the enclosure. Such aggressive-submissive interactions between given pairs of individuals were recorded and summarized and the results are given in Table I and show the dominance hierarchy. The deer are listed in the left hand column of

Table I according to position in the dominance hierarchy with the most dominant individual at the top and the least dominant at the bottom.

It will be noted that one of the eight-point bucks, B₁, dominated all of the females, while the younger eight-point buck, B₂, was dominated by all of the females during most of the summer when the antlers of the bucks were in velvet. The spike buck (Sp) was dominated by all of the does.

On August 30, B₂ was seen to dominate Dnd. It is possible that this was a permanent reversal because while no more interactions were observed, Dnd was not seen to dominate B₂ up to the time that observations ceased on September 4. The dominance relationship between the two does, Dnd and Pn, was somewhat unstable. On August 31 Dnd was seen to strike Pn with one fore foot and at once Pn reared up on her hind legs and gave a long low harsh sound, almost a hiss, meanwhile keeping the nostrils closed tightly; when Pn threatened Dnd in this manner the latter retreated. The next day Pn was again seen to threaten Dnd, rearing up on both hind legs, raising both forefeet and making a low harsh sound and at once Dnd retaliated and Pn retreated and left. These two does were seen to have seven aggressive-submissive interactions on the following day, all of which Dnd dominated while Pn failed to threaten back: Dnd was therefore adjudged to be dominant.

In conclusion, the White-tailed Deer in summer formed loose and variable groups, and this fact was associated with the presence of a definite dominance hierarchy based on frequent aggressive-submissive interactions of all the individuals.²

NYALA ANTELOPES.

Description of the Nyala Group. This group consisted of one adult male, one immature male, four adult females and one immature female about two-thirds grown. Identification of individuals was easy in the case of the mature and immature males because of the characteristic pelage and large horns of adult males and smaller horns of immature males. The females are hornless and resembled each other quite closely but could be readily distinguished by differences in markings. The various animals are here referred to as Scar (Sc), Dark Spots (Ds),

TABLE I.

Dominance hierarchy of the White-tailed Deer. Aggressive-submissive interactions between dominants and subordinates.

DOMINANTS	SUBORDINATES									
	B ₁	Wn	Bn	Sc	Dnd	Pn	Dnl	B ₂	Sp	
B ₁	—	4	31	24	15	24	5	27	14	
Wn	—	—	30	18	20	21	2	7	9	
Bn	—	—	—	23	7	16	11	13	18	
Sc	—	—	—	—	11	11	9	19	7	
Dnd	—	—	—	—	—	15	8	4	7	
Pn	—	—	—	—	1*	—	1	12	11	
Dnl	—	—	—	—	—	—	—	6	6	
B ₂	—	—	—	—	1†	—	—	—	4	
Sp	—	—	—	—	—	—	—	—	—	

* See text.

† Reversal August 30.

²Recently (March 24-25, 1950) through the courtesy and assistance of the Wisconsin Conservation Department I was able to visit the overbrowsed deer yards in the Flag River and Brule River valleys of northwestern Wisconsin during the critical part of winter. Here we observed definite signs of a dominance hierarchy among wild White-tailed Deer gathered about bales of hay put out to help save the deer from starvation. Adult bucks generally dominated all the other deer, whereas does and yearlings with a few exceptions dominated the fawns of the preceding year. Aggressive-submissive interactions were also frequent within each sex and age group. Fritz (1929, Board Game Commissioners, Bull. 12, pp. 31-35, Penn.) in overbrowsed deer range in Pennsylvania where the deer were not artificially fed, observed a group of deer that were browsing and noted that the older deer constantly chased away younger deer which as a result had difficulty in procuring much food. In both Wisconsin and Pennsylvania it has been noted that winter mortality is much greater for the fawns than it is for other age groups.

Long Spot (Ls), Adult Female (M) and Young Female (Y).

The history of the group was known only in a general way. The adult male and the oldest female (Ds) were the parents or grandparents of all the others and were brought from Africa in 1939. Young were born each year in the Zoo, usually in late December or January. The three adult females were daughters of the original female and two were about four years old and one about 3½ years old. The immature male was born in December, 1945, and was therefore about 2½ years old. The youngest female was only seven months old, having been born on January 1, 1947, to one of the daughters of Ds. The mother would not feed Y, and Y was thereupon transferred to Ds which was pregnant at the time, and later lost her own young one.

The enclosure or paddock known as the African Plains was roughly in the shape of a broad oval, some 325 feet in greatest length and 150 feet wide, comprising a little more than one acre. It was connected at one end with a corral about 100 feet long which adjoined a shelter house which the animals could enter at night. The paddock, like the corral, was covered with grass; it contained a few trees and a small, shallow pool near the center. A number of birds and other mammals shared the enclosure with the Nyalas.

Grouping Relations. In general the Nyalas formed a compact group within the paddock, particularly while resting. Generally they moved as a herd when going from one part of the paddock to another, or when going to the shelter house in the evening. Although they might scatter out somewhat while grazing, each member of the herd was usually less than 50 feet from some other member. The one exception to these grouping relations was the young buck, which was generally kept away from the group of females by the old buck. Occasionally the young buck was permitted to join the herd. The females seemed to associate with each other more closely than did any of them with either of the males during the period of observation.

TABLE II.

Dominance hierarchy of the Nyala Antelopes. Aggressive-submissive interactions between dominants and subordinates.

DOMINANTS	SUBORDINATES						
	Adult Buck	Young Buck*	Sc	Ls	Ds	M	Y
Adult Buck	—	35	4	4	2	1	2
Sc	—	—	—	6	1	13	1
Ls	—	—	1	—	6	2	30
Ds	—	—	—	—	—	1	—
M	—	—	—	1	—	—	—
Y	—	—	—	—	—	—	—

* Practically no aggressive-submissive interactions were observed between the young buck and the females.

Dominance Relations. The dominance hierarchy of the Nyala herd is illustrated in Table II. The adult male frequently lunged at the young buck with his horns and with head down, particularly when the latter came near him and the females, or when a piece of bread or carrot was thrown between the two bucks. The young buck invariably beat a hasty retreat, but since he generally returned near the group after a while, a good number of such aggressive-submissive interactions were observable. Occasionally the adult buck would gently push the females aside with his horns when they went after a piece of bread or carrot directly in front of him, but he never made the vigorous dash that characterized his actions toward the young buck. Even on the relatively few occasions when the young buck was feeding next to the females, practically no aggressive interactions were observed between the young buck and the females.

The females when very hungry and competing for food would butt a subordinate female away from the food with the hornless head, usually striking the subordinate on the flank. At times the subordinate would butt back; sometimes the two would spar momentarily with their heads before the subordinate receded.

The emphasis of this antelope study was placed on the female Nyalas since casual observations suggested the interesting possibility that they were not organized into a definite dominance hierarchy. The animals were then observed regularly from August 6 through August 12 for 30-minute observation periods which totalled four hours. When pieces of bread or carrots were thrown to them, two females would often put their heads close together and munch simultaneously at opposite ends of the same carrot or bread, but with no sign of aggressiveness. During these eight observation periods only one head butt was seen to occur between adult females.

These rare aggressive female interactions suggested the possibility that a dominance hierarchy might be revealed under adequate stress. Therefore, on August 13 and 14 the female Nyalas were penned in the small corral to one side of the main enclosure, where their foods were limited to grass and a little hay. After two days of limited food deprivation the female Nyalas were fed bread, carrots and some grain on the morning of August 15. The bread and carrots were thrown one piece at a time between various individuals. Within half an hour 24 aggressive-submissive interactions were seen among the adult females. Eight of these interactions were contested, i.e. a brief sparring bout with the heads took place. When one individual submitted the other was adjudged to be dominant, at least in that particular contest. All of the aggressive interactions among the adult females occurred with food as the incentive, and therefore the greatly increased aggressiveness of the fe-

males was related to their increased hunger after two days on restricted rations.

The female Nyalas were retained in the corral until the next day and observed for half an hour during the same time as in the preceding day. Pieces of bread and carrot were thrown to them as before, but only two aggressive-submissive interactions were observed. Indeed, only six such reactions were observed following the day the animals were put back on normal rations, in a total of four hours' observation from August 16 through August 23 (30-minute observation periods).

Table II shows that the adult female Nyala Antelopes demonstrate a dominance hierarchy when made hungry by limiting their food. The definiteness of this hierarchy is indicated by the fact that of a total of 31 interactions only two were reversals of the usual dominance order. However, the dominance order was unstable as indicated by the large proportion of the head butts which evoked some retaliation before one of the contestants would retreat.

In conclusion, the adult female Nyala combined a tendency toward close aggregation with a low degree of aggressiveness, since a dominance order was evident only under the stress of food deprivation.

PENGUIN COLONY.

Description of the Group of Penguins. This group contained 14 penguins: 10 Black-footed (*Spheniscus demersus*), 1 female Humboldt (*Spheniscus humboldti*) and 3 hybrids (*Spheniscus demersus* × *humboldti*).

Individuals were readily identified without the use of artificial markings. One of the two adult hybrids was known as Double-band (Db), the other as Single-band (Sb). An immature hybrid was denominated Light-head (Lh), an immature Black-foot was Dark-head (Dh).

The Penguin Enclosure, semi-circular in shape and approximately 40 feet in greatest width, was surrounded by a low, overhanging fence. The area possessed a rocky substratum; about one-half of it was occupied by a deep pool. Four nest boxes, floored with sand and with the open side facing the water, formed a row at one end. The area just in front of the nest boxes was also mostly covered with sand. No other animals were kept in the enclosure with the penguins.

Much of the history of the penguins was known. The group consisted of three original pairs and their Zoo-bred progeny. These three pairs in turn were the remnants of two groups which came in 1941 from the New York Aquarium, or directly from South Africa. One pair was composed of a Black-foot male (originally thought to be a female and named "Annie") which paired with a female Humboldt; the other two pairs were Black-foots. These three pairs had occupied the same nest boxes for several years. They will be referred to as Pairs 1, 2 and 3, and they occupied Boxes 1, 2 and 3 respectively.

Pair 2 was the interspecies pair. The fourth box was not regularly occupied, but a pair of hybrid adults (Pair 4), consisting of Db and Sb, occupied it more often than did any of the other pairs. Occasionally, however, when the box was empty, Pair 5, consisting of two Black-foots, B (for "Baldy") and Tp (for its characteristic black patch on the throat) would move in for a while. The sexes of Pairs 4 and 5, of the unpaired adults and of the immature birds, were all unknown.

The hybrids were of course the offspring of Pair 2 and included Pair 4 and the immature bird, Lh. Pair 1 birds were the parents of Pair 5. Dh was the offspring of Pair 3, and although it was six to eight months of age, it was still closely associated with them and was fed fairly regularly by the female, especially during the first part of the summer. The downy young of Pair One was called Y; this bird did not leave the nest box during the first half of the summer. Finally there was one small adult Black-foot of uncertain parentage which, like Lh, did not consistently associate with any other penguin and was quite often solitary; it was labelled S.

Grouping Relations. The dynamics of group formation in the penguins could not be completely worked out without experimental analysis but certain deductions seem justified by observation. Grouping depended (1) on the mechanisms responsible for sex-pair and family integration; (2) on the mechanisms responsible for interpair aggregation; (3) on physiological changes associated with the season, such as the moult; (4) on the daily routine to which the birds were accustomed; and (5) on territorial relations. These categories all overlap to some extent; territorial relations are of sufficient importance from the viewpoint of the present study to justify separate and detailed treatment.

It was noted that only members of a pair brayed when close together. Generally when the two birds of a pair were separated and one commenced to bray, the other would proceed directly to its mate, no matter in what part of the enclosure it happened to be, and the two would then bray together. Only members of a pair or their progeny ever preened each other—i. e., nibbled each others' head or neck feathers with the tip of the beak. As a rule only members of a pair engaged in mutual courtship. In the case of pairs with a dependent offspring, the feeding of the young one was a major force in family cohesion.

Interpair grouping seemed to be stimulated by hunger, by the coming of nightfall, and possibly by braying. When one pair brayed on its territory the other pairs were likely to go to their own territories to bray. Interpair grouping seemed to be somewhat inhibited or limited by the territorial organization of the colony and by individual variations in the time of bathing or general exploratory behavior. Male 2 ("Annie") was especially independent of the group.

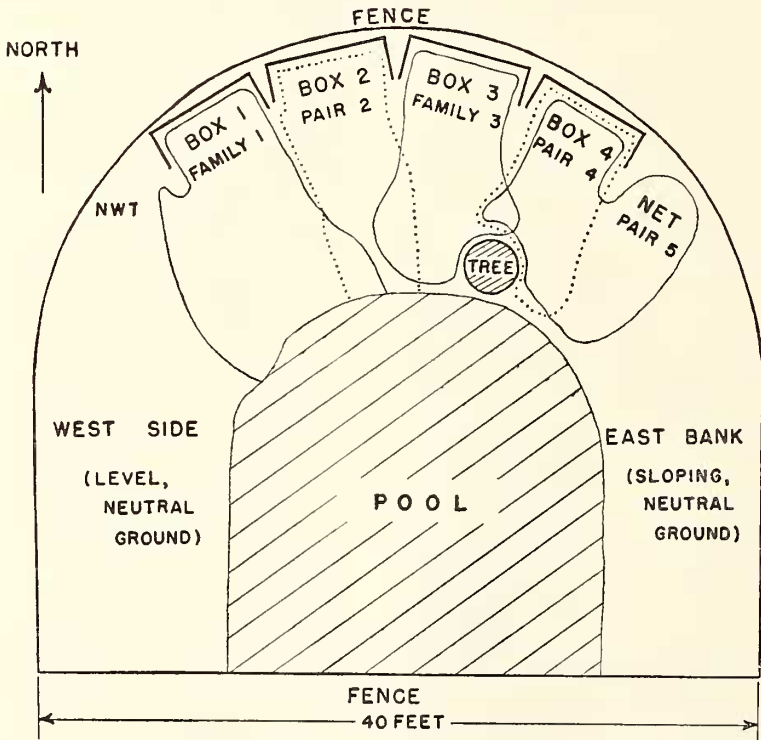
During the late summer the birds moulted, but as a rule only a few individuals at a time would moult. Moulting individuals often stayed apart from the others, away from their mates and territory. A moulting bird would stand quietly and, except at feeding time, seldom entered the water.

The grouping relations of the penguins varied to a considerable degree with their daily routine. Early in the morning most of the birds would bathe. They were generally fed between 9:00 and 9:30 A.M. and again at about 2:30 P.M., and they tended to organize their activities around these feeding periods. About one hour before each feeding they would leave their territories and assemble in a compact waiting group on neutral ground near the gate through which the keeper would enter with their fish. One of the Pair 1 birds would stay with their downy young one in the nest box until some time after the others had assembled, but it usually joined the group when the keeper approached. Occasionally it would vacillate between the effects of the two drives, first moving five or ten feet toward the group and then abruptly returning to its nest box and young one, only to repeat this procedure after a brief interval. Considerable aggression often occurred when the keeper arrived and the birds crowded closer to the fence and to each other. The fish were thrown into the pool and were devoured quickly; the entire feeding period lasted only 5 to 10 minutes. The

immature penguins, Y and Dh, usually were fed by their parents just after the adults had fed. Frequently Female One, the mother of the youngest penguin, Y, was the first bird to cease feeding, leave the pool and proceed toward her territory. After the feeding the birds would move into their own special territories and the excitement of the feeding period would merge into a period of braying which generally lasted about an hour. Courtship and a few attempts at copulation were usually observed at this time, as were territorial defenses as the birds readjusted themselves on their territories. In general the peak frequency of braying tended to precede that of courtship, while a period of courtship generally preceded attempts at copulation. Braying was contagious and quickly spread from one pair to another; Pair 3 generally initiated the braying of the colony.

These same general patterns of behavior were followed both morning and afternoon. During the forenoon and early afternoon as well as in the late afternoon and evening the birds would rest quietly within their territories for the most part, leaving only occasionally to bathe or swim in the pool or just to wander about the enclosure. At night they generally rested within their territories, but sometimes they would abandon them for neutral ground and rest there.

Territorial Relations. Text-fig. 1 is a map of the Penguin Pool. It shows the boxes



TEXT-FIG. 1. Territories defended by the penguins in the New York Zoological Park colony. NWT refers to Northwest Territory, NET to Northeast Territory. The boundaries of territories 1, 3 and 5 are indicated by continuous lines and those of territories 2 and 4 by dotted lines.

TABLE III.

Location of penguin territorial defenses. **T**=territory; **n**=north half but outside nest box; **s**=south half; e.g. T1n means north half of Territory 1; **Sh**=adjoining shore; **NET**=Northeast territory; **NWT**=Northwest territory. Vocal defenses are not included.

	In own box	T1n	T1s	T2n	T2s	T3n	T3s	T4n	T4s	NET	NWT	Sh1	Sh2	Sh3	Sh4
♂1	8	46	26	—	12	—	—	—	—	—	1	7	1	—	—
♀1	6	14	15	—	2	—	—	—	—	—	—	—	—	—	—
Y	1	—	2	—	—	—	—	—	—	—	—	—	—	—	—
♂2	6	—	2	18	6	1	3	—	—	—	—	—	2	—	—
♀2	0	—	—	1	3	—	—	—	—	—	—	—	—	1	—
♂3	1	—	—	3	3	10	11	1	2	—	—	—	—	—	—
♀3	2	—	1	4	11	14	14	—	—	—	—	—	—	—	—
Dh	—	—	—	—	—	1	2	1	—	—	—	—	—	—	—
Sb	2	—	—	—	—	—	2	1	2	1	—	—	—	—	—
Db	1	—	—	—	—	—	2	5	4	—	—	—	—	—	—
B	1	—	—	—	—	—	3	2	3	9	—	—	—	—	—
Tp	1	—	—	—	—	—	2	1	2	11	—	—	—	—	—

occupied by particular pairs or families and the territories which they often kept clear of other penguins. Table III gives the data on which this map is based.

Territories were defended by threatening movements, by vocalizations or occasionally by active attacks. Sometimes the defending bird seized and held the retreating interloper with its beak, while beating it with its flippers; the trespasser as a rule would manage quickly to escape. During the summer fights were very rare but when they occurred the birds would fence very rapidly with their beaks and beat each other with their flippers. Early in the summer Male Two lost one fight to Male One on the latter's territory, and won one fight with Male Three, but the exact site of the latter fight was not recorded. B won one fight over S on the neutral ground of the west side of the enclosure.

When one bird threatened another it would stretch its neck toward the intruder or advance rapidly and directly toward it and the latter would generally retreat at once, frequently going to its own territory. If the two territories adjoined the birds would sometimes bray or yell at each other. Sometimes the threatened bird, after retreating a step or two, would stop, tilt and twist its head so that the face and beak were horizontal, holding this pose for a few seconds. This attitude exhibited a conspicuous pink spot above the eye. Although the function of this pose was not clear it possibly serves to inhibit attack, since no observations were made of a bird being attacked while it maintained itself in this apparently very vulnerable position.

Cooperative attacks in non-vocal defense of the territory by the members of a pair were not common, and were observed only 17 times as compared with 329 defenses by

one or the other individual of a pair operating alone (Table IV). However, a definitely larger proportion of merely vocal defenses of the territory were cooperative, and the voice of one partner generally stimulated the other partner to bray, if it was in the vicinity. Because members of a pair often moved about more or less together, they sometimes trespassed and were driven off as a pair; 47 such occurrences were recorded (Table IV).

There were variations in the pattern of individual territories as depicted in Text-fig. 1. In general the territories centered about the nesting boxes, although comparatively few defense reactions within the nest box of a pair were recorded, compared with defenses of the north or adjacent half of the ground between the nest box entrance and the pool. In other words the birds were seen to defend their front yards much more often than they were seen to defend the interior of their houses from intrusion. One possible explanation for this is that whereas territorial boundaries outside the nest boxes were often violated during the ordinary daily movements of the birds, intruders seldom dared to enter a nest box with one or both of the owners in the box or nearby.

Pairs 1, 2 and 3 were older, more dominant and better established than any of the other pairs. In addition, Pairs 1 and 3 each had a young one. These three pairs defended their territories more often (Table III) and spent more time on their territories than did Pairs 4 and 5. These latter two pairs wandered about the enclosure a good deal and as a consequence were often attacked. Pair 4 moved more often as a pair than did Pair 5 and so were more often attacked as a pair (Table IV). Pairs 4 and 5 show considerable territorial overlapping, because both pairs

TABLE IV.

Individual penguins involved in territorial defenses. Trespassers in top row; defenders in column to left. Number of defenses is tabulated. Vocal defenses are not included.

	♂1	♀1	Y	♂2	♀2	♂3	♀3	Dh	Sb	Db	B	Tp	Lh	S	P ₁	P ₂	P ₃	P ₄	P ₅	Total
♂1	—	8	1	16	6	11	2	4	2	3	8	2	16	14	—	1	7	16	1	117
♀1	—	—	—	9	—	14	3	1	—	—	4	3	2	5	—	2	1	—	—	44
P ₁	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Y	17	—	—	1	—	1	—	—	—	—	—	—	—	3	—	—	—	—	—	22
♂2	1	—	1	—	—	2	3	1	1	2	4	2	7	9	—	—	1	6	1	41
♀2	—	—	1	—	—	—	3	—	—	—	—	—	1	3	—	—	—	—	—	8
P ₂	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	2
♂3	—	—	2	—	3	—	—	—	—	2	—	6	4	9	—	—	—	2	2	30
♀3	2	1	—	2	—	1	—	—	—	—	7	6	—	37	—	—	—	—	1	57
P ₃	—	—	—	—	—	—	—	—	—	—	—	—	3	1	—	—	—	—	—	4
Dh	1	—	—	—	—	—	—	—	—	1	1	1	1	3	—	—	—	—	—	7
Sb	—	—	—	—	—	—	—	—	—	—	1	—	2	2	—	—	—	—	1	6
Db	—	—	—	—	—	—	—	—	—	3	1	—	1	1	—	—	—	—	1	6
P ₄	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	2
B	—	—	—	—	—	—	—	—	—	2	—	—	3	1	—	—	—	—	—	6
Tp	—	1	—	—	2	—	—	—	—	—	—	—	—	4	—	—	—	—	—	7
P ₅	—	—	—	1	—	1	—	—	1	—	—	—	5	—	—	—	—	1	—	9
Total	21	2	4	28	11	29	11	6	4	9	28	21	50	92	0	1	12	26	8	

would defend Box 4 and the ground in front of it. This may well be related to the fact that during the preceding year B of Pair 5 was mated to one of the Pair 4 birds and occupied Box 4 with this bird. Pair 4 dominated Pair 5 and was able to evict Pair 5 from Box 4 and from the area just in front of the box. Perhaps as a result of this Pair 5 centered their defenses in the area called the Northeast territory which adjoined Box 4 and Territory 4. The two unmated adults, S and Lh, did not have any regular territory and very rarely did they bray, their rare vocalizations consisting merely of low moans.

In general territorial overlap was greatest in those parts of the territories near the shore of the pool away from the immediate vicinity of the nest boxes. There were several reasons for this: these areas were the usual resting places for most of the pairs, and they also formed a highway for overland movement to and from the neutral ground, particularly the West Side. Such movements facilitated contacts and most of the territorial defenses were seen in the period of readjustment following the general feeding periods in the morning and afternoon. The birds would defend the vicinity of their usual resting places and this made it appear as if they sometimes defended the adjoining parts of their neighbors' territories, particularly when the neighbors were absent from these areas. Pair 2 spent much of its time in Box 2 and Pairs 1 and 3, which often rested in the south part of their own territories, tended to spread their territories over the southern part of Territory 2. Another complicating factor was the frequent presence on the south part of Territory 2 of S, a

solitary, unmated and relatively young adult. The members of Pairs 1 and 3 dominated S, and as a result of the attempt of S to settle between them they often threatened and drove S. Any considerable overlap between Territories 3 and 4 was somewhat nullified by the presence of a large tree between the south parts of these two territories.

In contrast, territorial boundaries in a few places were very sharp, particularly between the north part of Territory 1 and 2. Male 2 was continually encroaching at this boundary and was as persistently driven back by one or the other of the Pair 1 birds. As a rule Pair 1 kept strictly out of the north half of Territory 2.

The two unmated birds, S and Lh, wandered about more than did any of the other birds, and were more often driven from the territories than were any of the mated birds (Table IV). Lh spent a relatively high proportion of its time in the pool, as compared with the other birds.

The males defended a more extensive area than did their female mates (Table IV) and in the case of Pairs 1 and 2 the males defended the territory much more frequently than did the female (Table IV). However, in the case of Pair 3 the female defended the territory much more than did the male. About one-half of the 112 observed territorial defenses by Male 1 were against other males showing interest in Female 1 or else against S and Lh which attempted to establish standing places near the south half of Territory 1. S tried to locate a little closer to Territory 3, and the great majority of the territorial defenses of Female 3 were against S. Most of the territorial defenses of Female

1 were against males apparently attempting to "flirt" with her, i.e., Males 2 and 3. These males seemed also to be attracted by the squeaking or "food-begging" vocalization of the young penguin in Box 1, and they would not infrequently move toward Territory 1 when Y was calling for food.

Of special interest are 17 threats or pecks directed by Y against his parent, Male 1. It is quite possible that these pecks are of actual territorial significance, since they occurred on Territory 1. Male 1 was in moult at the time and his appearance had changed considerably, while 60 mgm. of male hormone (testosterone propionate)³ had been implanted in Y. In contrast, Y directed none of his attacks against Female 1 which was not in moult. Female 1 was generally near Y so it is also possible that his attacks on his father were related to sex jealousy. Interestingly, Male 1 tolerated these attacks from his progeny.

Dh, the young penguin of Family 3, pecked at his mother 32 times and at his father 15 times on Territory 3, but these pecks were all associated with active food-begging by Dh and it seemed almost as if Dh were trying to attract the attention of his apparently indifferent parents. However, the aggressive behavior of Dh towards its parents could be interpreted in other ways, e.g. as food frustration, since Dh had apparently not yet learned to feed itself.

The penguin territories on the whole had been established for a long time. Territories 1, 2 and 3 at least were very stable and apparently did not often need to be defended by active threat or attack. On June 27, Family 1 was watched all day (16½ hours) and during this time Male 1 defended the territory only 6 times, Female 1 defended the territory only 8 times. All defenses occurred before 2 P.M. However, Male 1 on another day was once seen to chase a bird off his territory at 10:15 P.M., well after nightfall.

A certain degree of either general excitement or of specific drive is perhaps necessary for territorial defense. Very early one morning Male 1 was seen to permit Pair 4 to enter his box while he was inside lying on the nest. Pair 4 left but soon returned, and then repeated this behavior. Male 1 merely looked at them each time, but after the 4th intrusion he abruptly arose, seized one of the Pair 4 birds with his beak and beat it vigorously with his flippers. In fact all of the behavior patterns of the penguins were likely to be more or less fragmentary and incomplete at times apparently depending on the level of excitability reached by the birds as well as on other factors. Braying seemed to excite the birds, and one of the most effective of all stimulus situations causing territorial defense was the braying of trespassers on the territory. For example, one day Family 3 brayed on the south part of Territory 2 not far from their usual resting

place on Territory 3; at once Male 1 ran out of Box 1 into Territory 2 and threatened them. They stopped braying but stayed where they were and he returned to Box 1. When trespassers brayed while actually on Territory 1 Male 1 as a rule actively attacked them.

Certain incidents threw some light on the value of territory to penguins. For one thing it helps protect the nest. One afternoon while all the other penguins were in another part of the enclosure Male 1 was seen to enter first one undefended nest box and then another, each time removing some nest material (largely twigs) to his own box. He worked continuously and in 15 or 20 minutes had removed practically all of the nesting material in the colony to his own box. Another value of territorial establishment and maintenance was seen during the rare occasions when both parents of Family 1 left their young one all alone in Box 1. Male 2, and once Pair 2, thereupon entered Box 1 and bit the young one. Thus, territorialism relates to protection and survival of the young.

Dominance Order. Roberts (1940) observed some signs of possible dominance order in Gentoo Penguins in nature. At the New York Zoological Park it was found that the penguins had a definite dominance order while on neutral ground. The data are given in Table V, which tabulates the frequency with which any given penguin was seen to peck or threaten on neutral ground various other individuals which in turn retreated. The scarcity of such aggressive-submissive interactions is noteworthy; only 391 such interactions were recorded during some 126 hours of observation, an average of little more than 3 per hour. One reason for this was that the birds spent much of their time within their own territories. Another is the fact that food competition in the penguins seemed to have very little dependence on aggressive behavior, unlike the case in most other species of birds in which dominance hierarchies have been studied. The bird that could secure the greatest number of fish in the pool in the shortest time got the most, and the bucket of smelts as a rule disappeared within 5 or 10 minutes once it was emptied into the water. Fish placed on the ground were frequently ignored. It was, however, true that a relatively large proportion of the pecking and threatening took place in the highly excited group just before feeding. Reverse pecks or threats of a normally subordinate bird against a dominant bird were rare; such reactions were most likely to occur in the excited and crowded group just prior to feeding.

From Table V it is apparent that the three oldest males held the three highest ranks in the dominance order, while the youngest birds tended to be at or near the bottom. The three oldest females ranked fairly high. In a few cases dominance relations were not worked out, and in one case, that of Lh versus S, (both unmated birds), the dominance relations were apparently unstable.

³I am indebted to the generosity of the Schering Corporation, Bloomfield, N. J., for this hormone.

TABLE V.

Dominance order of penguins on neutral ground. Dominators in left-hand column, birds dominated in row above; frequency of aggressive-submissive reactions (pecks or threats plus retreat of other bird) are tabulated.

	♂1	♂2	♂3	Sb	♀1	♀2	Db	♀3	Lh	B	Tp	Dh	S	Y	Total
♂1	—	3	8	11	3	5	10	6	14	7	3	3	5	1	89
♂2	—	—	2	3	1	—	3	2	2	1	2	—	3	2	21
♂3	—	—	—	3	1	1	3	1	5	7	2	—	3	2	27
Sb	—	—	—	—	6	—	4	4	34	11	3	1	6	2	71
♀1	—	—	—	1	—	3	—	3	4	5	—	1	3	—	20
♀2	—	—	1	—	—	—	1	1	8	6	1	1	7	1	27
Db	—	—	—	—	—	—	—	1	7	7	3	1	1	2	22
♀3	—	—	—	—	—	—	—	—	6	3	2	—	3	—	14
Lh	—	—	—	—	2	—	4	—	—	17	9	2	8	4	49
B	—	—	—	—	—	—	—	—	2	—	—	—	10	1	14
Tp	—	—	—	—	—	—	—	—	3	—	—	—	7	2	12
Dh	—	—	—	—	—	—	—	—	—	—	1	—	6	1	8
S	—	—	—	—	—	—	—	—	11	—	—	—	—	2	13
Y	2	—	—	—	2	—	—	—	—	—	—	—	—	—	4
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The relations of the dominance order on neutral ground to fixed or established territories are of special interest (Tables IV and V). The three oldest males not only were at the top of the peck order but they also held, with their mates, the most stable and most frequently defended territories. The top bird in the dominance order, Male 1, defended the largest territory. The younger and unmated birds not only were at or near the bottom of the dominance order, but in addition they did not hold territory, although Lh and S tended to rest persistently in certain places. Pairs 4 and 5, which held unstable territories which they occupied and defended rather infrequently, were intermediate in the dominance order.

The territory-holding penguins defended their territories against birds higher in the dominance order 40 times in contrast to 284 defenses against birds lower in the dominance order. If we omit the 117 territorial defenses of Male 1 which was the top bird in the dominance order and which had no dominator, the number of territorial defenses against subordinates is reduced to 167, which is still more than four times the number of defenses against dominators. One reason why the penguins did not often defend their territories against birds above them in the dominance order is probably related to the relatively infrequent trespassing by the more dominant birds on the territories of the lower-ranking birds. The enclosure was so arranged that in coming and going by way of land to the usual resting and waiting place on the West Side, most of the penguins had to pass through territories of the dominant males rather than through the territories of

the relatively subordinate Pairs 4 and 5. However, the East Bank, also neutral ground, was frequently visited and quite often the birds would return overland to their territories, so this explanation is probably not sufficient to explain completely why territories were defended relatively infrequently against birds of higher rank in the dominance order. Male 3 was actually seen to retreat from threats of Male 2 on the territory of Male 3 on two occasions.

Occasionally the birds were seen to defend standing or resting places on what was normally neutral ground. One morning a small boy climbed into the enclosure to get his ball and in doing so he frightened the penguins over to the East Bank where they stayed in a group for well over an hour. Soon it was noticed that the birds were starting to defend the places on which they had settled, particularly when a bird attempted to change places. Subordinate birds even brayed at or threatened birds above them in the dominance order whenever the dominants moved near them. For example, Pair 5 brayed at Pair 1 which brayed back briefly; and when Male 3 moved near Pair 4, Sb brayed at him, Male 3 brayed back, and these two birds then exchanged threats and pecks, and again brayed at each other.

Many of the aggressions on neutral ground were by males. However, the males rarely or never pecked or threatened their mates although they spent far more time in close association with their mates than with any other birds. Occasionally the members of a pair were seen to clatter their beaks together while facing each other; it looked as if the birds were fencing rapidly with their

beaks. The interpretation of this behavior is not clear, although it has been considered as courtship behavior (Kearnton, 1930). However, the type of courtship behavior that is most frequent and which was seen to be followed by mounting and copulation, is different. Usually courtship is apparently initiated by the female which parades in an arc before the male with neck arched and beak lowered; the male follows and places his throat and beak closely over the head of the female and works his way behind her while gently slapping her front and back with his flippers, meanwhile vibrating his head and beak over the top of her head. When he gets around behind the female he keeps placing one foot on her back as if "urging" her to lie down; if she does so he will mount. This pattern may be prevented or brought to an abrupt end by the bill clatter which, it seemed, was often initiated by the female's raising her beak upward and so preventing the male from holding his head in the normal courtship position. The resemblance of the bill clatter to the fighting pattern of the birds suggests the possibility that instead of being courtship behavior it could well be interpreted as a form of aggressive behavior, possibly related to sex frustration.

It is possible that the normal greeting ceremony between male and female of a pair serves to inhibit attack. Roberts (1940) observed that a stuffed Gentoo Penguin placed on a nest with eggs or chicks almost invariably elicited the normal greeting bow and hiss of this species from whichever of the two owners returned first. The intruder was then attacked, presumably because it was unable to respond with similar behavior. On a few occasions Male 1 was seen to peck and drive his own mate, Female 1, out of Box 1 shortly after she had entered, and on one of these occasions it was noted that the bowing ceremony of the female was omitted; on the other occasion the female bowed twice, as did the male, but she held her head and beak very high afterward. Bowing seemed to bear some relation to the nest site since it was frequently omitted when the birds of a pair came together away from the nest after a period of separation. Mutual braying, however, was rarely omitted. Occasionally when mates came together the male proceeded at once to court the female, omitting both bowing and braying ceremonies.

One incident occurred which indicated that the male may occasionally defend his female mate. Male 2 often encroached on Territory 1 and one day while Male 1 was absent he was unusually persistent in approaching Female 1, who was attempting to feed her young. This persistence of Male 2 continually diverted Female 1 from her young one while she drove Male 2 back to his own territory. Male 2 seemed to become bolder and actually entered Box 1 and when Female 1 threatened him, instead of retreating out of Box 1 he pecked at her. Female 1

thereupon uttered a low moan and immediately her mate, Male 1, left the assembly of penguins on neutral ground some 20 feet away, ran to Box 1 and drove away Male 2.

Although cooperative braying by mates was common in vocal defense of their territories, actual cooperative threats on neutral ground were rare. One day Pair 4 were seen swimming side by side in the pool and braying at and chasing Male 2. One of the Pair 4 birds (not identified) actually pecked Male 2, which ordinarily dominated both members of Pair 4. Male 2 circled about and left the pool at the place where his own territory adjoined the shore.

The question arises as to the basis for high social rank in the penguins. Sex was one such factor, since the males generally dominated females. Age is another highly important factor—the oldest birds held the highest ranks. Large size was a possible factor and was roughly associated with high rank. The birds were not weighed, but the Humboldt female and her hybrid offspring, Pair 4 and Lh and the three top males 1, 2 and 3, which were about the same size, were the largest birds; Females 1 and 3, and Dh were definitely smaller birds, while the smallest of all were Pair 5 and S. While male sex, greater age and larger size were all associated in general with higher rank in the dominance order, to what extent each factor was directly meaningful for high social rank could not be decided.

In summary, the grouping pattern of the penguins depended to a large extent on their system of territorial relations as based on individual sex pairs or families. Important modifying factors were related to the dominance hierarchy, the daily routine of feeding, bathing and general movement about the enclosure, the attraction between birds of different pairs, and physiological seasonal changes such as the moult. The penguins showed no direct aggressive competition for food items, unlike the other animals studied at the New York Zoological Park.

THE FLOCK OF GESE.

Description of the Group. This group consisted of one Pink-footed Goose, six Barnacle Geese, one pair of Lesser Canada Geese, one pair of Cackling Geese and one pair of Black Brants. Late in the summer one pair of Blue Geese was added.

Identification of individuals within each species without marking them proved to be difficult, although the degree of development of the white collar at the base of the black neck was very helpful in the case of the Lesser Canada and Cackling Geese. At first aniline dyes were used to color some of the lighter portions of the plumage; most of the dye washed off within two or three weeks, and then colored leg bands were used.

The six Barnacle Geese came from a purchase of two in 1927, and a gift of five in 1942. They were kept in another enclosure where they reared four young in 1942 and

1944. In 1945 they were moved to the enclosure in which they were kept at the time of this study and subsequent mortality reduced them to their present numbers.

The Blue Geese were definitely larger than any of the other geese and they were removed from the enclosure in early spring because they had been aggressively driving the other geese about and apparently preventing attempts to breed by the latter. The Blue Geese were returned late in the summer after one pair of Barnacles had laid and made an unsuccessful attempt to rear young. The rest of the geese were present in the enclosure continually and, with the Blue Geese, all had spent the winter together.

The enclosure was roughly oval, about 225 feet long and 100 feet at its greatest width, comprising approximately $\frac{1}{2}$ acre. About one-half of the area was occupied by a pond. The rest contained a good scattering of shrubby and herbaceous vegetation as well as a number of small trees. The enclosure was merely fenced in at the sides and the birds were confined by wing-clipping. In addition to the geese and brant there were three Demoiselle Cranes, a South African Sheldrake and a Yellow-billed Duck in the enclosure, while a varying number of semi-domesticated Mallards and Black Ducks often flew into and out of the enclosure.

Grouping Relations. In general all of the geese were likely to come together while resting and sleeping and to a lesser extent while feeding, competitive intolerance in the latter activity preventing as close flocking as during the former. The flock as a whole could readily be recognized as being organized into sub-groups composed of the different species and sex pairs. Thus the Barnacles associated with each other more often and more closely in the non-breeding flock than they did with any of the other species. In turn, the six Barnacle Geese were divided into two pairs, each with one other individual adherent. Br (male) was mated to Bb (female) and Bg attached itself closely to this pair. Bp (male) possibly was paired with By, and Bu tended to be with them more often than with the other group of three Barnacle Geese, perhaps more through exclusion by Br than by preference for Bp and By. Unfortunately, only the sex of Br, Bb and Bp was definitely determined, nor were the former family relations of these geese known. Although the pair of Lesser Canada Geese, Lu and Lg, associated together more often and more closely than did either of them with any of the other geese, they did not form nearly so close a pair as did the two Cackling Geese, Cy and Cr. The two brants, Rbt and Bbt, like the two Lesser Canada Geese, were likewise a relatively loose pair.

It was found that one of the best ways to study the grouping relations of the geese was to map the distance between different individuals when they sat down to rest, as they usually did during the forenoon. Another method was to note which individuals

joined and left the main flock of feeding or resting geese in constant pairs or subgroups. Frequently certain individual geese wandered about the enclosure together but apart from the other geese. All of these clues, repeatedly observed, made it possible to decide the preferential grouping patterns of the geese. When this was done for all the geese there resulted the interesting hypothesis that the degree of association tended to parallel the degree of similarity in appearance of the species.

Lesser Canada and Cackling Geese, which very closely resemble each other and are considered races of the same species (A.O.U. Checklist of North American Birds, 1931), were more often together than with other species. In turn these geese associated more closely with the Barnacle Geese than they did with the Black Brants which have rather short necks for geese and lack white markings on the head; white head markings, although more extensive in the Barnacle Geese, were also present in Lesser Canada and Cackling Geese. The Pink-footed Goose, which resembled the others least of all, was most often apart from the main flock of the other geese.

It is possible that this general association pattern connects with the history of contiguity of these particular individuals rather than having any significance with respect to species recognition cues. However, a similar phenomenon was noted for five different species of pelicans which were confined to a $1\frac{1}{2}$ acre pond at the Zoo; in this group the more similar species roosted together each night. Thus the American and European White Pelicans, both predominantly white species, roosted together with the pale gray Dalmatian Pelican (from southeastern Europe and Asia) on the same rocky islet in the pond. The Eastern Black-backed Pelicans (Australia), which have black and white plumage, roosted together in another part of the pond, while several California Brown Pelicans roosted in various other places still more remote from the first group. These roosting spots were observed for some 20 different evenings and remained quite consistent.

The geese showed a strong tendency to engage in any given form of behavior as a group. For example, they would often feed more or less together, preen themselves at the same time, lie down and rest together and move about the enclosure together, either on land or in the pond. Occasionally they would splash about in a circle in the pond and these rather uncommon periods of increased activity soon tended to involve the entire group. It was as if almost any form of behavior was contagious and tended to induce the same type of behavior in all other geese.

Br, a male Barnacle Goose, was consistently followed by his mate, Bb, and by their hanger-on, Bg, as he moved about the enclosure. Sometimes the rest of the geese,

to be less tolerant of Bg than was Br during the summer's observation (cf. Table VI). Bb spent the night on her nest.

When the gosling hatched Br seemed to lose all interest in the nest site, but instead kept all the other geese away from the vicinity of Bb and her gosling with the same energy which he had previously devoted to the defense of the nest site. The gosling closely followed its mother about. She kept up a low grunting or grumbling sound, which was apparently the equivalent of the clucking of a broody hen, as she browsed about.

That the gosling was the stimulus to Br's excessive aggressiveness toward the other geese was demonstrated by an accidental incident which occurred the day after it hatched. On this day the gosling was found in another part of the Zoo by Headkeeper of Birds George Scott, who returned it to its parents. In the meantime, Br and Bb were observed by Mr. Scott to be flocking with the other geese, but the moment after their gosling was returned to them, Br and Bb at once drove off all the other geese and kept them from the immediate vicinity of the gosling.

The function of this aggressive isolation of the young from the other geese was demonstrated by the tendency of Bg, which was still often permitted to associate with Br and Bb, to peck and bite at the gosling. This was observed several times but the parents merely honked at Bg without attacking. Four days after the gosling hatched, Pf was seen to threaten the family—Br had lost the dominance over Pf which he had maintained with his territory, and from this time on to the end of the summer's observations Pf seemed to show a special antipathy to Br and Bb (Table VI). What their dominance relations to Pf had been before Br and Bb started nesting was not known. Whenever Pf threatened Br and Bb the gosling was likely to be left alone temporarily and when this occurred Bg was occasionally seen to bite the gosling. It seems not unlikely that these events were responsible for the death of the gosling, which occurred when it was six days old. Pf was seen chasing the parents which kept circling about a shrub that stood over the dead gosling. After the dead gosling was removed the parents moved about the enclosure for some time honking loudly at intervals of a few seconds, but later in the day they were seen to have rejoined the flock.

Dominance Relations in the Flock. Dominance was expressed by one bird advancing toward another, which it threatened with open beak, with head held low and with neck extended except for its base which was drawn backward slightly. Meanwhile the subordinate bird would retreat; rarely it stood its ground until attacked. The numbers of such reactions observed were tabulated and the results are shown in Table VI for all species of geese in the enclosure. About 11 per cent. of the threats were made on two individuals simultaneously, which were

usually a sex pair. Each such threat is tabulated separately for each of the two birds threatened.

It may be noted that dominance-subordination relations within the species and between species of geese were frequent and pronounced. It should also be noted that these dominance relations were consistent for any given pair of individuals and no reversals occurred during the period of observation, except for the territorial case already described.

From June 23 to July 18 a total of 14 hours of observation of the geese at various places in the enclosure, including the spot where they were usually fed, yielded a total of only 45 threats, including intra- and interspecies contacts. Thereafter, to facilitate observation of dominance relations, pieces of bread were tossed between selected geese in the period from July 21 to September 2. This covered a total of 16½ hours (not including the all-day observation on July 10) during which a total of 591 threats were observed between the geese. It is evident that placing the birds in a specific food competitive situation by means of this technique increased the frequency of aggressive interaction more than ten-fold.⁴ At the same time this method merely brought out the already existing dominance order, since none of the 45 aggressive-submissive interactions previously observed were at variance with the dominance relations observed during the later observation periods. These 45 encounters involved 24 of the 78 possible paired relations among the 13 geese of Table VI.

Several interesting relationships may be observed by inspection of Table VI. In this table the presumed sex pairs or mates are grouped together; i.e., birds which associated much more closely with each other than with other geese in the enclosure. The scarcity of threat reactions within sex pairs is noteworthy, particularly in the breeding pair of Barnacle Geese, Br and Bb, and in the pair of Cackling Geese, Cy and Cr. It is not evident from the table in the case of the pair of Lesser Canada Geese, Lu and Lg. However, it was not infrequently observed that when the Pink-footed Goose attacked Lg, that Lu would immediately attack Pf, often coming 10 or more feet to do so.

The tolerance of one mate for another is also of interest in view of the fact that only one pair of the geese made any attempt to breed. This pair, Br and Bb, were near the top of the dominance order in the flock as shown in Table VI, which for this pair includes only their *non-territorial* interactions with the other geese. The male, Br, delivered

⁴ An interesting parallel to this increase of aggressiveness with increased food competition has been observed under natural conditions, by R. C. Hopkins for Canada Geese on Horicon Marsh, a famous refuge for waterfowl in Wisconsin (1947, *Wis. Wildlife Res. Quart. Rpts.*, 6:14-23. Wis. Conservation Dept.). Numerous instances were noted during goose-trapping observations in which one goose chased another away from the corn used as bait. As the corn scattered in the vicinity of the trap became scarce the frequency of such aggressive-submissive interactions increased.

only one of his 117 threats (on individual birds) on his mate, Bb, despite the fact that special effort was made to establish the dominance relations within this pair; e.g., as many as 30 successive pieces of bread were tossed between them without the aggressive result that almost invariably followed this procedure when Br was near some other goose. Tolerance of one bird for its mate is apparently related to the degree of association permitted, and the birds assumed to be mates were the ones that in general kept company most often. Br and Bb tended to keep more closely together than did any of the other pairs of geese; this fact, together with an apparent antipathy of Pf for the pair, helps account for a large number of joint avoidances of Pf by this pair which were observed.

Another fact of interest is that each of the mated birds seemed to dominate much the same subordinates as did its mate; Lorenz (1935) has maintained that in flocks of geese the female assumes the social rank of the male to which she becomes mated. It can be seen from Table VI, furthermore, that the female, Bb, and Cr (of unknown sex) initiated few aggressive interactions, and were much less aggressive than were their respective mates. These birds belonged to the two most closely integrated pairs among the geese.

Frequency of threat reactions considered alone may not be a particularly good index to the intensity of dominance relations. For example, Bg was often threatened by Br and Bb because of the insistent tendency of Bg to associate with this pair. Bg was often driven off but persistently returned. Actually the other Barnacle Geese were tolerated less since they were usually attacked by Br at a much greater distance than he permitted to Bg, and so mere tabulation of the frequency of threats taken alone gives a false picture of the relationship. Bp and By received a relatively small number of threats, one reason being that they usually made off soon after bread was thrown to the geese or else they stayed to one side and did not compete very actively for the food. In contrast, Bu made little effort to avoid the other geese, actively competed for bread morsels, and was therefore often threatened by the other geese. Bp was a male Barnacle Goose of moderately high dominance status. It limped badly and initiated very few aggressive interactions, yet its subordinates were never seen to make any attempts to attack Bp.

From Table VI it may be seen that one intraspecies triangular arrangement existed with reference to the dominance relation, i.e., By dominated Bu, which dominated Bg, which in turn dominated By. An example of an interspecies triangle is the domination of Br by Pf, of Pf by Lu, and of Lu by Br. There was a rough association between body size and rank in the dominance hierarchy. The order of body size from largest to

smallest was: Pink-foot, Barnacle, Lesser Canada, Cackling and Brant.

In summary, the non-breeding flock of geese moved freely about the enclosure and their grouping patterns were based on sex pairs and on larger subgroups. The more closely integrated pairs were characterized by a very low degree of intrapair aggression. In the feeding aggregation the degree of association of given individuals, other than sex pairs, was related to precedence according to the dominance hierarchy, and was also related to the species. In the non-feeding aggregations, subgroups other than sex pairs were associated with degree of similarity in plumage coloration of the different species and subspecies. A general factor causing aggregation in all the geese was the tendency to engage in the same type of activity at the same time.

One pair of very dominant Barnacle Geese attempted to breed and isolated itself from the other geese, which were aggressively kept away from the vicinity of the incubating female by the male and later from the vicinity of the young by both parents.

DOMINANCE RELATIONS OBSERVED IN OTHER SPECIES IN THE ZOOLOGICAL PARK.

In the Goose Enclosure. Semi-wild Mallards and Black Ducks frequently flew into and out of the goose enclosure and were apparently dominated by all of the geese. Even the two Brants which were at the bottom of the goose dominance scale were each seen to threaten a Black Duck on separate occasions. Only very rarely did the ducks make any attempt to compete with the geese for food. The ducks themselves showed evidence of a dominance order, e.g., a female Mallard was seen to drive a Black Duck away from the feeding place one day.

Present in the enclosure were three Demoiselle Cranes, two of which were marked on the shoulders with green or red aniline dyes; they were designated G (green), R (red) and U (unmarked). They competed actively with each other and with the geese for the bread thrown into the enclosure. Cranes threatened other cranes or geese by advancing with partly opened bill, head low and slightly drawn back ready to jab, and at the same time they often uttered a harsh, rattling threat note. Crane G was at the top of the crane dominance order and was seen to dominate Crane R 86 times and Crane U 75 times. Crane R dominated Crane U 11 times.

Dominance Relations in the Flying Cage. The zoo has a very large flying cage, rectangular in shape, with an arched roof. It is approximately 150 feet long, 75 feet wide and 75 feet high. About half the floor area is occupied by a shallow cement-bottomed pool. A great variety of water birds were quartered in this cage. These birds were fed pieces of fish during the late afternoon; it was at this time that I sometimes observed

TABLE VII.

Dominance relations of certain wading birds of the southeastern United States as seen in a large flying cage. Dominators are listed to the left, subordinates are given in the row above.

	American Egret	Reddish Egret	Roseate Spoonbill	Snowy Egret	Night Heron	White Ibis	Scarlet Ibis
*4 American Egret	19	9	4	3	4	1	0
2 Reddish Egret	—	2	3	0	4	2	1
4 Roseate Spoonbill	5†	2†	4	9	0	5	3
3 Snowy Egret	—	—	—	19	6	4	1
2 Black-crowned Night Heron	—	—	—	—	0	0	0
6 White Ibis	—	—	—	—	—	6	5
3 Scarlet Ibis	—	—	—	—	—	—	0

* Number of individuals of each species.

† These interactions involved the same individual spoonbill.

them and recorded aggressive-submissive interactions.

Most of the aggressive-submissive interactions over the fish were observed in the wading birds, and a tabulation of the numbers of these interactions for species which occur in the southeastern United States revealed an interspecies dominance order (Table VII). The dominance order showed a rough parallel to the order of general size differences between the species. However, the dominance order did not strictly follow species lines. These birds were not marked but it was possible to distinguish certain individuals by size and plumage differences and thus to ascertain that in some cases dominance depended more on the individual characteristics than on the species characteristics. For example, the American and Reddish Egrets dominated two of the four Roseate Spoonbills, but the largest spoonbill dominated the American Egrets and at least one Reddish Egret as well as the other spoonbills.

Three to six individuals of each species of wader listed in Table VII were present in the cage, except for the Reddish Egrets and Black-crowned Night Herons of which there

were two each. It is of special interest that most of the observed aggressive-submissive interactions of the American and Snowy Egrets were intraspecific. The same was true of the Water Turkeys of which there were some half dozen individuals present; 20 of their 27 aggressive-submissive interactions involved another Water Turkey, and definite signs of an intraspecies dominance order were observed.

Many other birds were present in the cage. As a rule the herons and ibises seemed to dominate the Laughing and Herring Gulls, Water Turkeys and Tree Ducks, although they did not often come into direct contact with these species.

One of the interesting general features of the aggressive behavior patterns of these water birds is that much the same pattern was used regardless of the species at which it was directed, e.g., a Snowy Egret would erect its crest, neck and body plumes in a sparring match whether its threat was directed against a Roseate Spoonbill, a Silver Gull or another Snowy Egret.

Dominance Relations of Birds and Mammals in the "African Plains" Enclosure. Various species of birds and mammals lived

TABLE VIII.

Dominance relations of certain African mammals and birds as observed in a large enclosure. Dominants listed in column to left, subordinates in row above. Figures refer to number of aggressive-submissive interactions.

	Maribou	Blesbok	Ostrich	Imm. Nyala buck	Female Nyala
*1 Adult male Nyala	6	3	7	35	11
2 Maribou Stork	—	3	27	18	11
1 Adult male Blesbok	—	—	0	5	7
1 Female Ostrich	—	—	—	1	6
1 Immature male Nyala	—	—	—	—	1
4 Female Nyala	—	—	—	—	31

* Number of individuals.

TABLE IX.

Dominance relations between certain storks and cranes of the African Plains enclosure. Dominants listed to left, subordinates in upper row. Figures indicate number of aggressive-submissive interactions recorded.

	Maribou	European Crane	Crowned Crane	Demoiselle Crane
*2 Maribou Stork	0	1	3	1
2 European Crane	—	0	8	30
4 Crowned Crane	—	—	2	1
9 Demoiselle Crane	—	—	—	2

* Number of individuals.

in the Zoological Park's large, moated African Plains enclosure. While the animals are at complete liberty within the confines of the area, species tended to remain more or less together. Dominance relations were recorded by noting and tabulating the number of aggressive-submissive reactions over introduced food, generally consisting of bits of bread or pieces of carrot which were thrown into the enclosure.

Table VIII reveals that a dominance order may involve both mammals and birds, and that some but not all individuals of one species may dominate individuals of another species. For example, the adult Nyala buck was at the top of the dominance order, whereas the immature Nyala buck and the female Nyalas were dominated by the Maribous, Blesbok and, less definitely, by the Ostrich.

Of special interest are the high degrees of aggressiveness of the Maribou Storks and the low degrees of aggressiveness of the female antelope. These several species of birds and mammals occupy overlapping ranges in Africa.

There were in addition to the mammals mentioned above four female Bushbuck and one female Reedbuck present in the African Plains enclosure most of the summer. These small antelope were dominated by the Maribous and Ostrich but they generally did not enter into active and aggressive food competition with the other species of antelope and few of their dominance relations to these were established.

Table IX illustrates the dominance relations of the storks and cranes of the African Plains enclosure. The European Crane and Demoiselle Crane both breed in Europe and may winter in northeast Africa. The ranges of the Maribou Stork and Crowned Crane are more southerly but extend northward into northeast Africa.

This dominance order roughly parallels the size of the birds. The Maribous have very large beaks which reinforce their aggressive disposition. The small Demoiselle Cranes generally avoided the Maribous, so practically no aggressive-submissive interactions were recorded between these two species. It should also be noted that the two species at

the top of the dominance order, i.e., the Maribous and European Cranes, each consisted in this instance of a closely integrated pair of individuals.

Early in the summer the European Cranes nested and hatched out two young within the enclosure. While one parent sat on the nest the other would stand guard nearby and try to keep all other birds and mammals away from the vicinity of the nest. The female Ostrich was frequently chased 20 or 30 feet or more. When the adult Nyala buck grazed close to the nest the male European Crane placed himself between his mate and the antelope and with his beak pointed skyward indicated his disturbance by repeated loud trumpeting. He did the same when the Maribous approached. They did not retreat, and perhaps his inability to dominate them was fatal to one of the young, since the Maribous were later seen pulling at its dead body, which one of them swallowed. When keepers entered the enclosure to remove the remaining young bird to safety, both parent cranes feigned injury. This behavior pattern had not been seen when the safety of the nest or young was previously threatened by other birds or mammals living in the enclosure.

Dominance Relations of Certain Mammals in Other Large Enclosures. The importance of dominance for precedence to mates among antelope was well seen in the case of an adult male Indian Blackbuck which spent much of its time keeping six or seven immature bucks away from a sizable herd of females. This particular buck had killed his predecessor, as well as some of the immature males.

Mr. Irwin Katz (1949) was able to demonstrate the existence of a dominance order in a small herd of Barbary Sheep in a large outdoor enclosure in the Zoological Park. The males dominated the females and young; the males are heavier and have much larger horns than do the females.

No detailed study of the dominance relations of any of the carnivorous mammals at the New York Zoological Park was attempted. Cooper (1942) observed a dominance hierarchy among lions in a large outdoor enclosure at a lion farm in California. Among piscivorous mammals a dominance hierarchy has been described for captive Bottle-nose

Dolphins at the Marine Studios in Florida (McBride and Hebb, 1948).

Mode of Expression of Aggressive Behavior. Considerable structural adaptations to special conditions may exist without greatly altering certain patterns of aggressive behavior; thus biting or threatening with the beak was observed in such birds as geese, herons, spoonbills and ibis with very diverse beaks. Many birds retain the old reptilian pattern of hissing. At the New York Zoological Park or in other zoos and localities the following birds were heard to hiss either as a threat against other birds or as a defense against human beings: Ostrich, Rhea, Jabiru Stork, White Stork, European Bittern, Graylag Goose, Mute Swan, Ring-necked Pheasant, various vultures, young domestic pigeons and young Wood Pigeons. Others have recorded hissing in comparable stimulus situations for the following: Gentoo Penguin (Murphy, 1936), Cormorant, Capercaillie, Red Grouse, Common Partridge, Black Guillemot, Scops Owl, Barn Owl, Hoopoe (young), Wryneck and European Cuckoo (Witherby, et al., 1943). Interestingly enough, young Homing Pigeons in the nest, but not the parent, would hiss at my intruding finger. Passerine birds as a group have highly developed voices, and records of hissing seem to be rare in this order. However, the Blue Tit is said to hiss on the nest when disturbed (Coward and Blyton, 1941). The White Stork is practically voiceless, but uses both hissing and bill clattering as a threat. Among mammals, the primitive Platypus is said to hiss occasionally under stress (Holmes, 1939).

Several species of antelopes were observed to interlock their horns in sparring for an opening, and it is possible that the peculiar shape of the horns of many species is in part to be explained by evolution of species-specific interlocking patterns. The horns of the White-tailed Gnu curve forward, those of the Brindled Gnu sideways, and the behavior patterns when these animals would hook the bars of their cages differed in corresponding fashion. The fixity of the behavior pattern that corresponds to a special type of horn was demonstrated repeatedly by a Beisa Antelope of aggressive disposition in which the very long horns had been sawed off near their base. When its neck was touched lightly it would at once go through the complex stereotyped motion of thrusting the horns. It never made any effort to butt with its head, but apparently depended on the horns which it no longer had.

In summary, dominance hierarchies based on aggressive behavior were observed in species of a wide variety of bodily conformations and habitat types. These animals were maintained in relatively large enclosures. Intraspecies dominance hierarchies were observed by the author for Black-footed Penguins, various geese, Demoiselle Crane, White-tailed Deer and Nyala Antelope; by others for Barbary Sheep, Lions and Bottle-

nose Dolphins. Interspecies dominance hierarchies were observed for various large wading birds, geese and ducks; the same hierarchy may include both birds and mammals, as was observed for various African species.

The pattern of aggressiveness varies to some extent with special structures, as seen in the correlation of type of horn with a given type of fighting pattern in certain antelopes. The occurrence of reptile-like hissing in many orders of birds as well as in some mammals indicates a conservative element in the evolution of aggressive behavior patterns.

DOMINANCE HIERARCHIES IN UNCONFINED BIRDS AND MAMMALS.

On the basis of observation revealing the general occurrence of dominance hierarchies in confined animals, an investigation was made of the literature concerning the occurrence of such hierarchies in unconfined animals. Some of the earlier results of this effort have been reviewed elsewhere (Collias, 1944).

Intraspecies dominance hierarchies have been described for wild or unconfined birds in the following species: breeding groups of Sage Grouse on the dry plains of the western United States (Scott, 1942); Wild Turkeys in mixed hardwood and coniferous forest (Mosby and Handley, 1943); Ring-necked Pheasants wintering in a marsh overgrown with vegetation, (Collias and Taber, 1948); California Valley Quail along wooded streams bordering farmlands (Howard and Emlen, 1942); and a number of perching birds of woodland, farm, village and garden, including the very sociable Jackdaw (Lorenz, 1931) and winter flocks of Black-capped Chickadees (Odum, 1941, 1942), Blue Tits (Colquhoun, 1942), Tree Sparrows and Slate-colored Juncos (Sabine, 1949). In the breeding season most species of birds establish territories which they defend usually with considerable success from other members of their species, but Mrs. Nice (1943, p. 93) and Armstrong (1947, p. 285) cite many intraspecies instances, from penguins to passerines, of individual intruders dominating or even evicting other individuals from the territory of the dominated bird.

Mammals in which intraspecies dominance hierarchies under free-ranging conditions have been recorded include large herbivores like the zebra on the plains of Africa, (Alverdes, 1935), Mule Deer bucks in the coniferous mountain forests of California (Dixon, 1934), Red Deer in a Scottish forest (Darling, 1937); large carnivores like the Wolves and Grizzly Bears of Mount McKinley in Alaska (Murie, 1944; p. 28, p. 202); various small gnawing mammals such as the Wild Rabbit in England (Southern, 1948), the Golden-mantled Ground Squirrel and certain Chipmunks of the western United States (Gordon, 1940); and such primates as Gibbons (Carpenter, 1940), Rhesus Monkeys

(Carpenter, 1942), and Chacma Baboons (Zuckerman, 1932). Howler Monkeys probably have a dominance social gradient of low slope (Carpenter, 1942b).

Interspecies dominance orders have been recorded, usually somewhat incidentally, for various water and land birds. Among the ducks and geese on a park lagoon in Chicago (Jenkins, 1944) the following order was observed: a family of Blue Geese, Canada Geese, another pair of Blue Geese, Snow Geese, Mallards, Wood Ducks and Scaups. In this case, however, the adult Blue Geese and the Snow Geese were wing-clipped. Roughly, this is the order of size differences, except that the closely organized family of Blue Geese was able to dominate the much larger, more numerous and relatively unorganized Canada Geese.

The Ringed Penguin exercises aggressive dominance over the Adelie and the Gentoo Penguins in places in the Antarctic where these three species nest together (Murphy, 1936, p. 408). In the tropical rain forest of the Panama Canal Zone the aggressive little Striped Flycatcher has been seen to evict the much larger Oropendula from its nest, which the flycatcher may then appropriate for its own use (Chapman, 1929, p. 111-118). In the tropical forest of British Guiana, Beebe (1917) observed that hummingbirds feeding at flowering trees may attack other species of hummers, centering their attack more on some species than on others (p. 115); and he also noted that King Vultures always took precedence to carrion over other local species of vultures, such as the Yellow-head Vulture (p. 110).

The existence of interspecies dominance orders among birds that inhabit our woodlands, woodland borders, farms, villages and gardens is rather widely known because of the prevalence of *winter* feeding stations. In 1929 Mrs. Nice published her observations of such a hierarchy among certain winter birds in the central United States. In general, the order judged from precedence to food and aggressive interactions was as follows: Mockingbird, Cardinal, Harris Sparrow, Lincoln Sparrow, English Sparrow, and Field Sparrow. Sabine (1949) has recently described an interspecies dominance order in which different individual Juncos and Tree Sparrows were arranged in a triangular relationship with respect to each other. Colquhoun (1942) in Great Britain has noted an interspecies dominance order at a winter feeding hopper, including nuthatches and various species of titmice.

During the *spring* of 1948, at a pile of corn in a marsh near Madison, Wisconsin, it was observed that the male Red-winged Blackbird, which had established his territory at that spot, dominated the Song Sparrow which also had his territory in about the same place. Both of these birds with their mates eventually fledged young. They dominated the local Swamp Sparrows, a Catbird and a migrant White-Throated Sparrow.

Most of these contacts were observed repeatedly (previously unpubl.).

Small passerine birds may also show dominance relations at a feeding station during the *summer*. Dr. William Beebe reports the following observations:

"A continual daily supply of sunflower and other seeds attracted birds to a flat rock in a garden near Wilmington, south central Vermont. From July 22nd to 30th a few notes were made on peck dominance or tyrannization among several species and varying ages. . . . The general order of dominance, checked and rechecked day after day, was as follows: 1- Indigo Bunting, 2- Adult male Purple Finches, 3- Juncos, 4- adult White-throated Sparrows, 5- Song Sparrows, 6- White-crowned Sparrows, 7- Immature White-throated Sparrows, 8- Immature Purple Finches, 9- Chipping Sparrows.

" . . . Neither size nor abundance of individuals had anything to do with this order of tolerance. If we consider the sequence from dominant to submissive as 1 to 9, we find the corresponding order in respect to size, from the smallest up, to be: 9, 1, 3, 2, 8, 5, 4, 7 and 6. The same scale in abundance from rarest is: 1, 6, 4, 4, 9, 5, 3, 7 and 8.

"Occasional temporary shifts in dominance order were occasioned by the individuality of some single bird. One Song Sparrow fought steadily for his rights with all above him, and one immature Purple Finch had to be physically assaulted before he would give way."

In general interspecific dominance hierarchies seem to parallel gross size, but this rule is subject to some marked exceptions. For example, Kingbirds will go far from their nest site to attack a much larger bird like a Crow or Red-tailed Hawk (Davis, 1941), and small birds may gang up together on an owl or cat.

There is, of course, nothing absolute about any of these various interspecies dominance hierarchies as given here. Apart from their existence, it is of interest that so much variation results from differences in age, sex, territorial relations and other individual differences.

In summary, dominance hierarchies based on aggressive behavior have been observed in unconfined birds and mammals of a wide variety of species and habitats. *Intraspecies* hierarchies have been observed in land and water birds, and among fish-eating, carrion-feeding, seed-eating and insectivorous birds. Among mammals *intraspecies* dominance hierarchies have been observed in forest and grassland, herbivorous and carnivorous, cursorial and arboreal types. *Interspecies* dominance hierarchies have also been observed for birds of a wide range of habitat types as well as for those from diverse geographic localities, including species from polar and equatorial regions, temperate woodland and tropical jungle, desert and the ocean. Interspecies hierarchies have been observed dur-

ing the breeding and the non-breeding seasons for passerine birds.

Such observations, although not always as detailed as one would like, indicate that the existence of dominance hierarchies based on aggressiveness is one of the more general principles of social life among birds and mammals, and therefore one of the general problems which the different species of birds or mammals must face wherever they live together in a community.

SOME GENERAL COMPARISONS AND CONCLUSIONS.

Field and laboratory studies exert a reciprocal influence. Field studies provide a basic orientation but are often difficult and in such cases fruitful working hypotheses may be derived from laboratory studies. Thus the present study indicates that a fruitful field endeavor would be the detailed observation and study of the dominance relations within and between various species of wild birds on a pond or of the wild animals at an African waterhole.

The evidence which has been presented indicates that dominance hierarchies based on aggressive behavior are of widespread occurrence in different ecological types of birds and mammals in the field and in captivity.

Dominance hierarchies, like territorial relations, are also of widespread occurrence from a phylogenetic point of view. Both types of dominance patterns have been recorded in all the classes of living vertebrates, from the bony fishes to mammals, except for the Amphibia (Collias, 1944). Recently, Dr. A. F. J. Portielje of the Amsterdam Zoological Garden informed me that he had observed vigorous and persistent fighting between individuals of the Japanese Giant Salamander (*Megalobatrachus japonica*) in the aquarium of this zoo. This salamander is relatively primitive compared to other living amphibia and the occurrence of aggressive behavior in some of the more primitive members of various classes of living vertebrates makes it probable that such behavior is a primitive vertebrate attribute; it has been recorded for the Lake Lamprey among jawless forms (Noble, 1938), for *Amia* (Reighard, 1903) among the bony fishes, for *Sphenodon* (Gadow, 1901) among the reptiles, and for *Ornithorhynchus* (Burrell, 1927, p. 92, 166-167; Fleay, 1944, p. 74) among mammals.

Aggressive behavior, apart from predator-prey relations, has also been described for members of such important invertebrate groups as cephalopods (cf. Tinbergen, 1948), decapod crustaceans (Allee and Douglass, 1945; Douglass, 1946), spiders (Bristowe, p. 498-502, 1941), and insects including ants, bees, wasps (Wheeler, 1939; Pari, 1948), chalcids, butterflies, various dipterous flies, crickets, grasshoppers, stag beetles (Richards, 1927) and Hercules beetles (Beebe, 1947). Aggressiveness among invertebrates may be expressed in relation to dominance hierarchies,

territorialism or sex competition. These phenomena are therefore not restricted to vertebrates, but the present evidence indicates that this is a rich field for the investigator of invertebrate behavior (Allee, 1950).

Aggressive behavior is most likely to be displayed when one animal invades the territory of another, or in the case of dominance hierarchies, between individuals in which the dominance relationship is unsettled. Such cases of unstable dominance relations were observed within every group studied at the New York Zoological Park, but on the whole were rare. Yerkes (1943) has written that among captive Chimpanzees contests for social supremacy may be brief and decisive, or long continued and indeterminate, particularly in the case of evenly matched contestants (p. 48).

The tendency to form aggregations is even more widespread among both vertebrates and invertebrates than is the phenomenon of aggressive behavior (Allee, 1931, 1945; Collias, 1944). This has raised the problem of the nature of the relationship between these two apparently antagonistic forms of behavior. One solution providing for increased group coherence has been the increase of intragroup tolerance associated with a decrease of individual aggressiveness, as in the case of the female Nyala Antelope. The more aggressive and more loosely aggregated does of the White-tailed Deer provide a contrasting case. A related solution has been increase in specific intragroup tolerance associated with extragroup aggressiveness as in the sex pairs of birds such as penguins and geese. Another common type of solution, particularly among birds, has been the territorial isolation of the breeding pair from the rest of the group.

In general, the birds that held territories were also high in the dominance hierarchy, for example, the Barnacle pair, Br and Bb on the goose pond, Pairs 1, 2 and 3 in the penguin colony, and the European Cranes in the African Plains enclosure. These same pairs were relatively well integrated compared to other pairs of birds in the same enclosures. However, they were also relatively heavy in body weight, so it is not clear which of the correlations are causal in nature. Lack (1940) placed two pairs of British Robins and two pairs of Chaffinches in a fair-sized aviary; only the dominant pair of each species bred.

The effective protection and welfare of the young may require a rather high degree of dominance by the parents. Thus, inability of a parent to dominate an aggressor resulted in attacks on the young, as described for the penguins and Barnacle Geese. The same thing was also seen for an Indian Peafowl driven from her young one by a Marabou Stork. Katz (1949) observed in the Barbary Sheep that a ewe of low dominance status was often excluded, together with her lamb, from the food place for prolonged periods of time.

Simultaneous attack on a common enemy possibly helps integrate a group to some extent. Such cooperative aggression by two individuals of the same species on a third animal was observed for pairs of Black-footed Penguins, Roseate Spoonbills, Snowy Egrets, Australian Black-backed Pelicans, Maribou Storks and Himalayan Tahrs. Intraspecies aggressive behavior by groups above the level of the sex pair acting more or less as a unit has been recorded for a few species of birds and a few species of non-primate mammals, but seems to be particularly characteristic of the higher primates (cf. Collias, 1944).

Various other factors serve to increase the aggregating tendency under different conditions and have been reviewed in detail elsewhere (Collias, in press).

A little evidence gathered in this study supports the general idea that competition is more intense within than between species. Thus the American Egrets, the Snowy Egrets and the Water Turkeys, although caged with many other species of birds, were observed in aggressive encounters with members of their own species much more often than with members of other species. According to Howard (1920), territorial encounters in birds seem to be more frequent in the same or related species. Carpenter (1942b) has made a quite similar case for primates: "I have seen howlers feeding in the same trees with capuchin monkeys, gibbons feeding in the same tree with langurs. I have never observed organized groups of the same species peacefully associated. One may generalize by saying that among monkey and ape societies, intra-species competitions and group antagonisms are much stronger than between groups of different species or genera."

SUMMARY.

A. Dominance and grouping patterns were studied in small groups of selected mammals and birds kept in large enclosures at the New York Zoological Park of the New York Zoological Society.

1. A group of White-tailed Deer consisting of 6 does and 3 bucks had a dominance hierarchy reinforced by frequent aggressive-submissive interactions. In association with their aggressive nature the individuals were often scattered widely about the enclosure.
2. A group of 5 female Nyala Antelope, which normally showed no apparent aggressive interactions, moved about usually as a compact herd unit. An adult buck accompanied the females and generally kept a smaller, immature buck at some distance from the females.
3. A colony of 14 penguins (mainly Black-footed Penguins) were organized chiefly on the basis of individual pair territories. However, a dominance hierarchy existed on neutral ground.

4. A small flock of several species of geese had a dominance hierarchy with specific tolerances and subgroups based in large part on sex pairs within the larger flock.

B. Competition for food, and breeding success were related to the dominance hierarchies observed.

1. By restricting the unaggressive female Nyala Antelope to short rations for two days an unstable dominance hierarchy was made evident or developed.

2. By introducing specific pieces of food for which the geese competed, the number of observed dominance-submissive interactions was increased more than ten-fold.

3. Successful breeding was associated with high social rank in the penguins; and failure of a dominant pair of Barnacle Geese to breed successfully was apparently due to their inability to dominate one other goose in the enclosure.

C. Interspecies dominance hierarchies were found to exist among various water birds, as well as among certain species of birds and mammals from the African veldt. In addition to general size of species, rank in these hierarchies varied with age, sex, territorial relations and other aspects of individuality. In some of the water birds aggressive-submissive encounters occurred at a higher rate within the species than between species.

D. Tendency to aggregate was associated with degree of difference in coloration and pattern of plumage in the case of different species of geese and pelicans and also with the tendency for various individuals of the same or related species to engage in the same type of activity at the same time, in all groups studied.

E. Comparison of the results obtained at the Zoological Park with recorded instances of grouping patterns and dominance hierarchies among various species in nature indicates that the results of these observations in a zoo to a certain extent will have applicability to natural situations and should provide favorable working hypotheses for field studies.

BIBLIOGRAPHY.

- ALLEE, W. C.
1931. Animal aggregations: a study in general sociology. Chicago: University of Chicago Press. 431 pp.
 1945. Human conflict and cooperation: the biological background. Chap. 20, pp. 321-367, of "Approaches to National Unity". Fifth Symposium of the conference on science, philosophy, and religion. Edited by L. Bryson, L. Finkelstein, & R. M. MacIver. New York: Harper & Bros.
 1950. Extrapolation in comparative sociology. *Scientia*, 43: 135-142.

- ALLEE, W. C. & DOUGLIS, MARJORIE B.
1945. A dominance order in the hermit crab, *Pagurus longicarpus*. *Ecology*, 26: 411-412.
- ALVERDES, F.
1935. The behavior of mammalian herds and packs. A chapter in Murchison's Handbook of Social Psychology. Worcester, Mass.: Clark Univ. Press.
- AMERICAN ORNITHOLOGISTS' UNION.
1931. Check-list of North American Birds. 4th ed. 526 pp. Lancaster, Pa.: American Ornithologists' Union.
- ARMSTRONG, EDWARD A.
1947. Bird display and behaviour. London: Lindsay Drummond, 431 pp.
- BEEBE, WILLIAM.
1917. Tropical wild life in British Guiana. Vol. I, Part I. 290 pp.
1947. Notes on the Hercules beetle, *Dynastes hercules* (Linn.), at Rancho Grande, Venezuela, with special reference to combat behavior. *Zoologica*, 32: 109-116: 4 pls.
- BRISTOWE, WILLIAM SYER.
1941. The comity of spiders. London: Bernard Quaritch, Ltd. 560 pp.
- BURRELL, HARRY.
1927. The Platypus. Sydney, Australia: Angus and Robertson Ltd. 227 pp.
- CARPENTER, C. R.
1940. A field study in Siam of the behavior and social relations of the gibbon (*Hylobates lar*). *Comp. Psychol. Monog.*, 10(2): 1-168.
1942a. Sexual behavior of free ranging rhesus monkeys (*Macaca mulatta*). 2. Periodicity of estrus, homosexual, autoerotic and nonconformist behavior. *Jour. Comp. Psychol.*, 33: 143-162.
1942b. Societies of monkeys and apes. *Biol. Symp.*, VIII: 177-204.
- CHAPMAN, FRANK M.
1929. My tropical air castle. Nature studies in Panama. New York: D. Appleton & Co. 417 pp.
- COLLIAS, N. E.
1944. Aggressive behavior among vertebrate animals. *Physiological Zool.*, 17: 83-123.
— Social life and the individual among vertebrate animals. (in press). Annals New York Academy of Sciences.
- COLLIAS, NICHOLAS E. AND TABER, RICHARD D.
1948. Grouping and dominance relations among wild Ring-necked Pheasants. *Anat. Rec. (Suppl.)*, 101: 44-45.
- COLQUHOUN, M. K.
1942. Notes on the social behaviour of blue tits. *Brit. Birds*, 35: 234-240.
- COOPER, J. B.
1942. An exploratory study on African Lions. *Comp. Psychol. Monog.*, 17(7): 1-48.
- COWARD, T. A. AND BLYTON, ENID.
1941. Birds of the Wayside and Woodland. London and New York: Frederick Warne and Co.
- DARLING, F. F.
1937. A herd of red deer. London: Oxford Univ. Press. 215 pp.
- DAVIS, DAVID E.
1941. The belligerency of the Kingbird. *Wilson Bull.*, 53: 157-168.
- DIXON, JOSEPH S.
1934. A study of the life history and food habits of the mule deer in California. *Calif. Fish and Game Bull.*, Vol. 20, nos. 3 & 4. 146 pp.
- DOUGLIS, MARJORIE B.
1946. Interspecies relationships between certain crustaceans. *Anat. Rec. (Suppl.)*, 96: 57-58.
- FITZSIMONS, F. W.
1920. The natural history of South Africa. Vol. 3, 278 pp. London: Longmans, Green & Co.
- FLEAY, D.
1944. Observations on the breeding of the Platypus in captivity. *Victorian Naturalist*, 61: 74-78.
- GADOW, HANS.
1901. Amphibia and reptiles. Cambridge Natural History. Vol. 8, 668 pp. London and New York: Macmillan and Co.
- GORDON, K.
1940. Territorial behavior and social dominance among Sciuridae. *Jour. Mammalogy*, 17: 171-172.
- HOLMES, CHARLES H.
1939. Australia's patchwork creature, the Platypus. *Nat. Geog. Mag.*, 76: 273-282.
- HOWARD, H. E.
1920. Territory in bird life. London: John Murray. 308 pp.
- HOWARD, W. E. AND EMLEN, J. T.
1942. Intercovey social relationships of the Valley Quail. *Wilson Bull.*, 54: 162-170.
- JENKINS, D.
1944. Territory as a result of despotism and social organization as shown by geese. *Auk*, 61: 30-47.
- KATZ, IRWIN.
1949. Behavioral interactions in a herd of Barbary Sheep (*Ammotragus lervia*). *Zoologica*, 34: 9-18.
- KEARTON, CHERRY.
1930. The island of penguins. New York. 223 pp.
- LACK, D.
1940. Observations on captive robins. *Brit. Birds*, 33: 232-270.
- LORENZ, K.
1931. Beiträge zur Ethologie sozialer Corviden. *Jour. f. Ornith.*, 79: 67-127.

1935. Der Kumpan in der Umwelt des Vögels. *Jour. f. Ornith.*, 83: 137-213, 289-413.
- MOSBY, HENRY S. AND HANDLEY, CHARLES O.
1943. The wild turkey in Virginia. Richmond: Pittman-Robertson Projects. Division of Game. 281 pp.
- MURIE, ADOLPH.
1944. The wolves of Mount McKinley. Fauna of the National Parks of the United States. Fauna Series No. 5. 238 pp.
- MURPHY, ROBERT CUSHMAN.
1936. Oceanic birds of South America. Vol. I. Amer. Mus. Nat. Hist., N. Y. 640 pp. 2 vols.
- NICE, MARGARET MORSE.
1943. Studies in the life history of the Song Sparrow. 2. The behavior of the Song Sparrow and other Passerines. *Trans. Linn. Soc. N. Y.*, 6: 1-329.
- NOBLE, G. K.
1938. Sexual selection among fishes. *Biol. Rev.*, 13: 133-158.
- ODUM, E. P.
1941. Annual cycle of the black-capped chickadee. I. *Auk*, 58: 314-333.
1942. Annual cycle of the black-capped chickadee. III. *Ibid.*, 59: 499-531.
- PARDI, L.
1948. Dominance order in *Polistes* wasps. *Physiological Zool.*, 21: 1-13.
- REIGHARD, JACOB.
1903. The natural history of *Amia calva* Linnaeus, Mark Anniversary vol., pp. 57-109. New York: Henry Holt & Co.
- RICHARDS, O. W.
1927. Sexual selection and allied problems in the insects. *Biological Reviews*, 2: 298-364.
- ROBERTS, BRIAN.
1940. The breeding behavior of penguins with special reference to *Pygoscelis papua* (Forster). British Graham Land Expedition, 1934-37. *Scientific Reports*, 1(3): 195-254. British Mus. Nat. Hist.
- SABINE, WINIFRED S.
1949. Dominance in winter flocks of Juncos and Tree Sparrows. *Physiological Zool.*, 22: 64-85.
- SETON, ERNEST THOMPSON.
1929. Lives of game animals. Garden City, N. Y.: Doubleday, Doran & Co., Inc. Vol. 3, Pt. 1. Hoofed Animals. 412 pp.
- SCOTT, J. W.
1942. Mating behavior of the sage grouse. *Auk*, 59: 477-498.
- SOUTHERN, H. N.
1948. Sexual and aggressive behavior of the Wild Rabbit. *Behaviour*, 1(3-4): 173-194.
- TINBERGEN, N.
1948. Social releasers and the experimental method required for their study. *Wilson Bull.*, 60: 6-51.
- WHEELER, W. M.
1939. Essays in Philosophical Biology. Cambridge, Mass.: Harvard Univ. Press, 261 pp.
- WITHERBY, H. F., et al.
1943. The handbook of British birds. V vols. London: H. F. & G. Witherby, Ltd.
- YERKES, ROBERT M.
1943. Chimpanzees. A laboratory colony. New Haven: Yale University Press. 321 pp.
- ZUCKERMAN, S.
1932. The social life of monkeys and apes. New York: Harcourt, Brace & Co., 356 pp.